Early Journal Content on JSTOR, Free to Anyone in the World

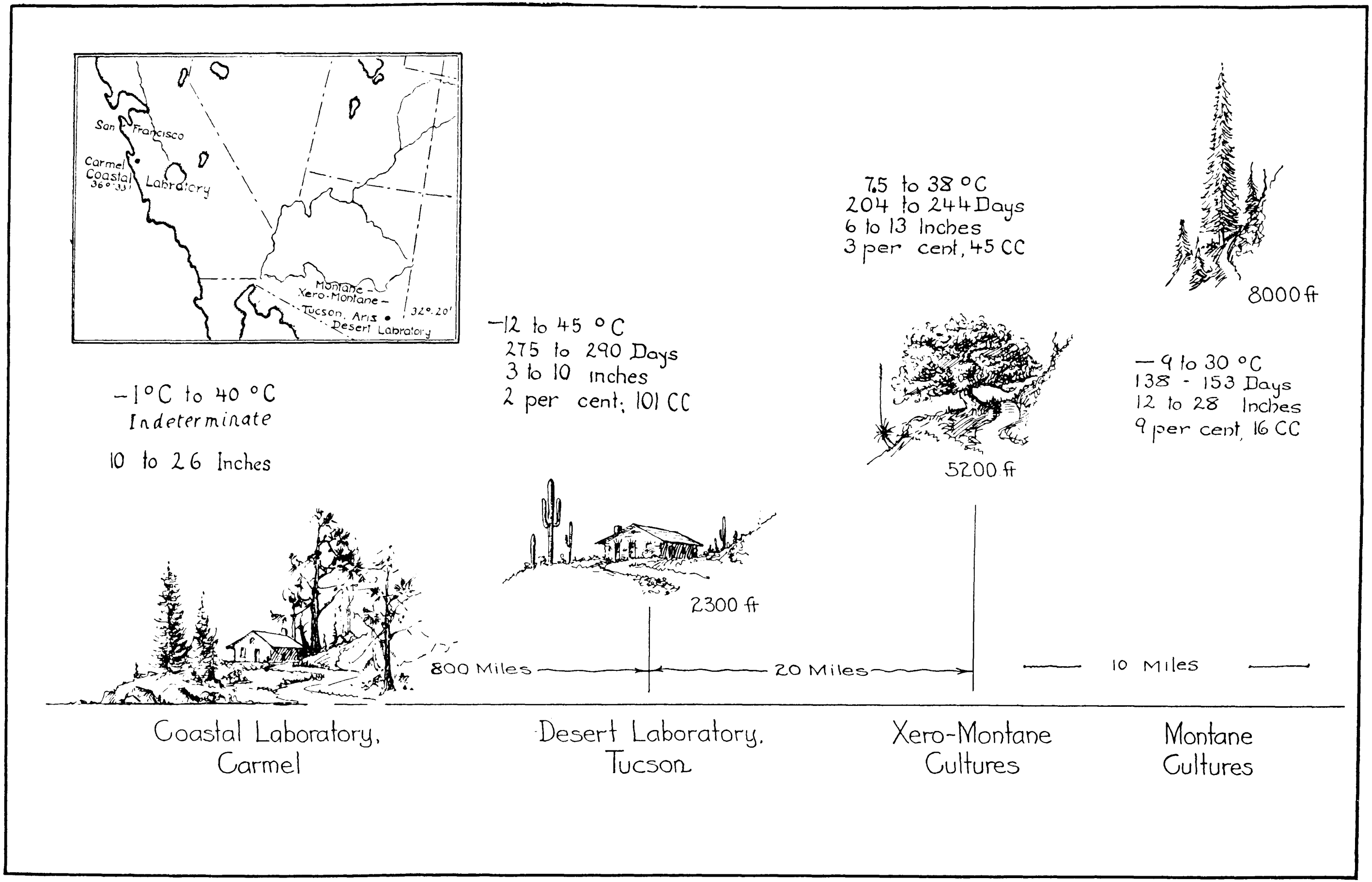
This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.



FRONTISPIECE. Sites of experimental cultures, showing relation to each other. For each site are given: 1st line, range of temperature; 2d line, length of growing season; 3d line, rainfall during the growing season; 4th line, percent of soil moisture, and average daily rate of evaporation in cubic centimeters from a Livingston atmometer, during three to five summer months.

ECOLOGY

Vol. II JANUARY, 1921 No. 1

THE REACTIONS OF PLANTS TO NEW HABITATS[1]

D. T. MacDougal

Carnegie Institution of Washington

Plan of Investigation

In May, 1906, Prof. B. E. Livingston and the writer ascended the Santa Catalina mountains, which rise to a height of about 3,200 meters across the valley to the northward of Tumamoc hill, on which the Desert Laboratory is located, for the purpose of selecting a site for a small plantation which was to be one of four to be used for comparative cultures in a desert valley, on a desert mountain and in a coastal region. The pack animals carrying the field equipment also bore a small collection of bulbs, rooted plants and seeds which were to be used in starting the first of the above series of experimental plots. This was done in a well-shaded ravine near melting snowbanks at an elevation of 2,500 meters, and an examination was made of the greater part of the pine-clad area of the range, covering an area of a few square miles for a suitable site. The final selection was made in November, 1906, at which time a small alluvial area in a valley opening to the eastward on the southern side of the culminating dome of the range, Mt. Lemmon, at an elevation of about 2,500 meters, was fixed upon as the site of a montane plantation.

The plan of the investigations included the establishment of small experimental areas in three or four places in which the environmental complexes were widely different (see frontispiece), the introduction of species from outside localities, and the exchange of species native to the localities of the experimental plots.

Three of the experimental areas were in connected physiographic series so that one was in the coniferous forest on the crest of a range, a second in the mid-slopes among the oaks, and the third in the desert valley at the foot of the range. By this arrangement the tests might be expected to yield direct information on the dissemination of the local species and on the barriers to distributional movements. In addition all three areas were used to test the behavior and survival of species from distant regions in which they were habituated to different environmental conditions. The fourth plantation was located near the shore of the Pacific Ocean in a cool, equable, foggy, coastal climate, at a distance of nearly 1,300 km. from the first three plantations. The observations and experiments in the coastal plantation were directed chiefly to studying the effects of the long cool growing season on plants from deserts, from mountain summits and from eastern America.

---

[1] Presented before the joint session of the Association of American Geographers and Ecological Society of America at Chicago on December 31, 1920.

The list of introductions is given in full on pages 9–15, as some of the species may yet escape, and unless their existence in the region were authenticated might become a source of confusion to the plant geographer.

The Montane plantation, as it is termed, has been characterized by the author in previous notices as furnishing an equivalent of forest climates of Michigan or northern New York (see fig. 1). The entire range of temperature at this place was between a winter minimum of —9° C. and a summer maximum of about 30° C. The growing or frostless season varies from 138 to 153 days, opening May 15 to 25 and closing October 10 to 15, as observed from 1909 to 1914. The rainfall during the growing season, or summer, of the period of 1908 to 1914 gave an average of 18.43 inches, ranging from

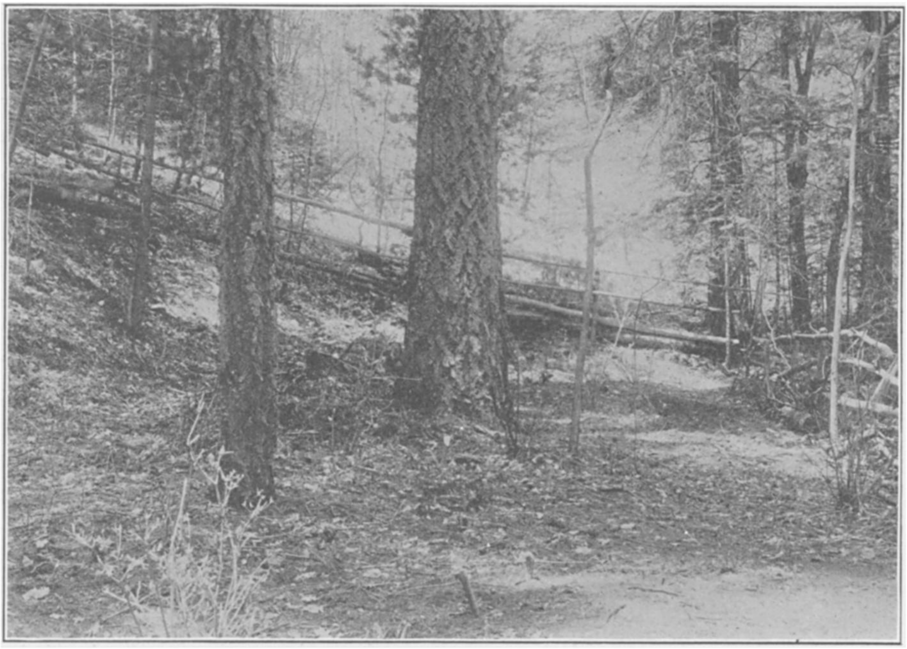


FIG. 1. Montane plantation, lower enclosure. Trees are *Abies concolor, Pinus arizonica, Robinia Neo-Mexicana, Acer brachypterum* and *Alnus oblongifolia;* shrubs include *Symphoricarpus oreophilus.*

11.40 to 27.82 inches. The soil moisture, at a depth of 15 cm., for April, May and June, calculated from north and south slopes, gave an average of 9.3 percent. The daily average evaporation from Livingston standard atmometers on north and south slopes for May to September was 16.44 cc.[2]

A second experimental location, known as the Xero-Montane, was selected at 1,700 meters in the encinal or region of sclerophyllous shrubs and trees, in which pronounced aridity prevails (fig. 2). This plantation was at the junction of two washes where the soil was a coarse alluvium. The temperature ranged from 7.5° C. to 38° C., the growing season was 204 to 244 days, the opening varying from April 1 to April 20, and the closing from November 10 to November 30. The summer rainfall varied from 6.05 inches to 12.51 inches, with an average of 8.88 inches. The soil moisture at a depth of 15 cm. at one station slightly lower was 3.3 percent, and at one slightly higher was 2.6 percent; the daily average evaporation at these two stations from Livingston standard atmometers was 48.3 cc. at the lower and 41.1 cc. at the higher during the period of May to September inclusive.

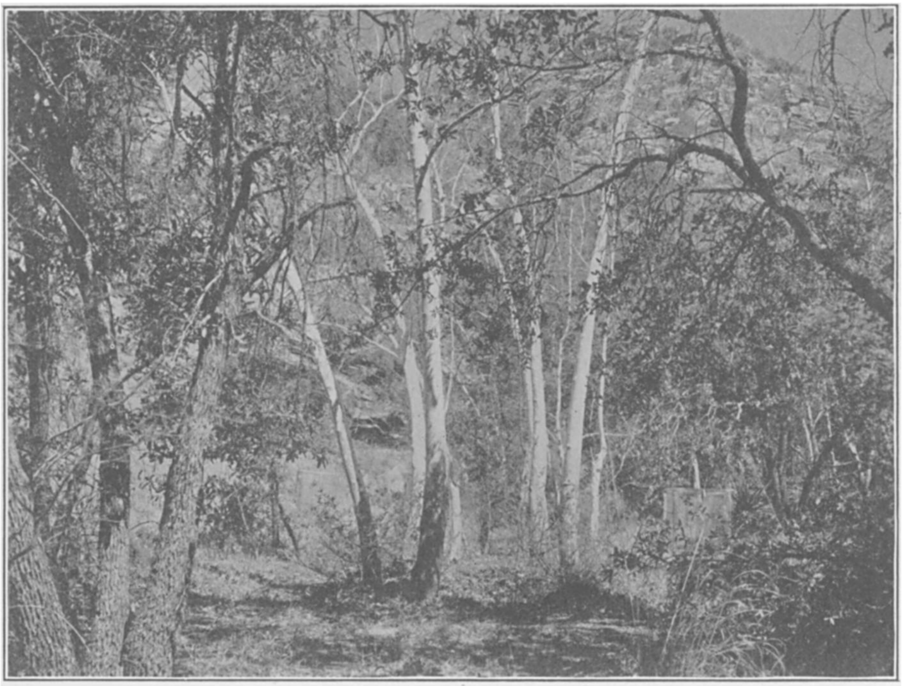


FIG. 2. Xeromontane plantation, showing trees of Quercus and Platanus; wire screen cage in lower right is to protect cacti from rodents.

The plantings at the Desert Laboratory were made in two places, one near the main building on the north slope of Tumamoc hill at about 850 meters and the other in alluvial soil at the base of the hill at 700 meters, in a place subjected to extreme action of cold air drainage (fig. 3). The temperatures at both places reach a maximum of about 45° C., while the minima of the upper location is — 12° C. and that of the lower place may drop to — 15° C. The growing season varies from 275 to 290 days, opening from March 1 to 10 and closing December 10 to 15. The summer rainfall averages 9 inches, varying from about 3 to 10 inches, the total annual being 12 + inches. The soil moisture for April, May and June averages 2 percent, and the daily average evaporation from May to September from Livingston standard atmometers is 101.1 cc.

---

[2] Shreve, F., "The Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors." Publ. 217 Carnegie Inst. of Wash. 1915.

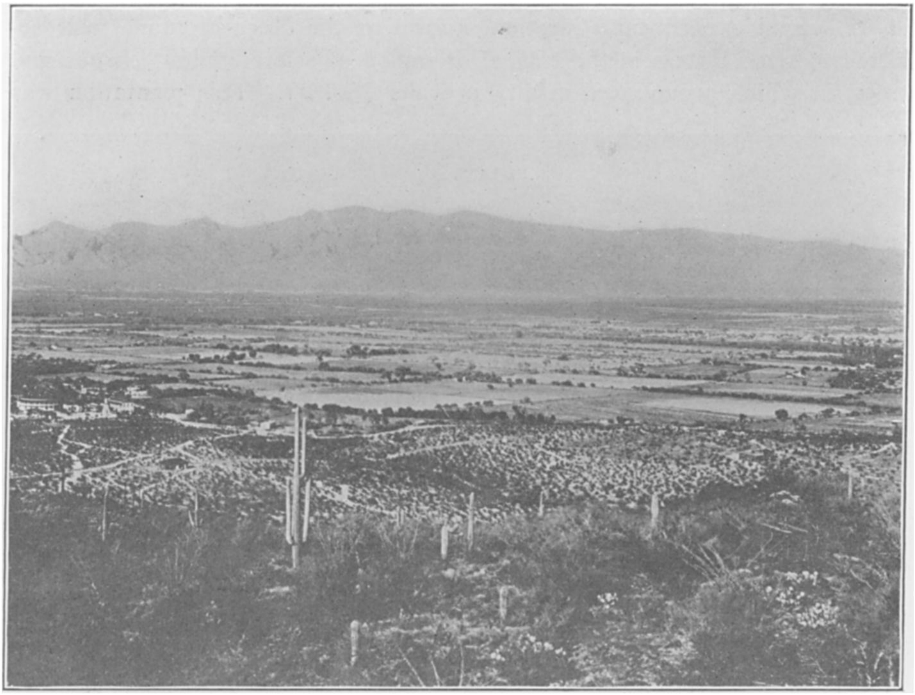


FIG. 3. View from the Desert Laboratory across the valley to the Santa Catalina Mountains on which the Montane and Xeromontane plantations are located. Desert vegetation in the foreground.

The three places are in 32° 30′ N. Lat. and stand in such topographical relation that many agencies would be constantly carrying seeds and propagules from the higher to the lower, and others would be less effective in dissemination in the opposite direction. Opportunities were, therefore, afforded for definite analysis of the interferences or modifications of the distributional factors, as will appear in the detailed descriptions following.[3]

---

[3] For description of physiography and geology see Blake, W. P., in "Botanical

All of the locations described are arid in greater or less degree, all are characterized by sudden changes of wide amplitude of the climatic factors, and all offer an environmental complex in which the course of the season and sequence of critical intensities is of greater importance than any series of summations or averages (see frontispiece).

The establishment of the Coastal Laboratory in 1909 made available a fourth set of conditions for comparative cultures at Carmel, California. This locality is within a few hundred meters of the shore of the Pacific in 36° 33′ N. Lat. This part of the coast is characterized by long continued heavy summer fogs, which in mid-summer sometimes obscure the sun for ten days or more. Temperatures from 1909 to 1920 have ranged from — 1° C. to 40° C. The lowest temperatures come in January and February, and secondary minima of 6° C. occur in July. The maxima generally come in September or October, although observed in May in some years. Seasons in the accepted sense are indeterminate, except that the heaviest rainfall generally comes in December, January and February, there being no mid-summer precipitation. The annual total ranges from 9.63 to 26.21 inches. The habitats tested included dry sandy soil and pools; no soil moisture or evaporation tests were made. The loose sandy soil has a low surface moisture content, with the result that the cessation of a cloudy or foggy period will be followed by marked wilting or flagging of species with broad leaves.

Species from the eastern United States were introduced into as many of the plantations as seemed to offer promise of survival, but especial attention was paid to the transfer of native plants from one to the other, as it was possible in this material to follow more closely the changes in general habit and morphogenic alterations.

productive cycles under conditions differing from those of the complex of the original habitat was one which demanded consideration at all stages of the work.

Removal of plants from their habitats to bring them into cultivation under conditions to which they were unaccustomed is exactly what occurs in the maintenance of the vast collections in the larger botanical gardens. The custodians of such collections frequently make note of the altered aspect of species after being incorporated in the growing collections, but the available amount of well-founded information is very slight.

Naturally in the organization of a research scheme of this kind one would turn to the classical experiments of Bonnier. The results obtained by him in the comparative culture of species in alpine and lowland regions in France furnished some new facts of interest and disclosed some morphogenic pos-

The matter of survival or capacity for completing the vegetative or re-

Features of North American Deserts," MacDougal, D. T., Publ. 99 Carnegie Inst. of Wash. 1908.

sibilities.[4] The obligations of the modern experimentalist in dealing with this subject are more severe, however, and the advance of knowledge in genetics, in soil physics, and in the environmental relations of plants make it more difficult to go into widely inclusive generalizations as to adaptive modifications and heredity than it was thirty years ago. Thus, for example, the mechanical division of a rootstock may not give actual identity of the second generation in separated cultures, and the removal of quantities of earth from one place to another may not secure unchanged substratum, since the chief soil factors are in themselves so largely a function of climate. The difficulties in the way of making exact analyses of the effects of such alterations in habitat conditions as those implied in the following cultures are in fact enormous, and the conclusions which may be reached are at best no more than inferential. The importance of the subject, however, and the interest which may attach to any results which yield new viewpoints or make possible new speculations are well worth any ordinary expenditure of energy or attention.

Plants Tested and Survivals

The records of behavior of the separate species have been kept with adequate accuracy from the time of their introduction, which in some cases extends over a period of 14 years, and the duration of the tests is illustrated by the fact that trees of Juglans now producing nuts were introduced as nuts in the beginning of the experiments.

The observations have been carried to a stage in which a comprehension of climatic complexes as barriers has been gained, and a conclusive demonstration of an animal barrage has been found. The relative value of seeds and of various types of resting shoots has been notably illustrated by the results of the observations on survivals of bulbs, tubers, corms, etc., and various departures in habit and morphogenic procedure have been induced.

The plants were put in the experimental plots at the season deemed most favorable for their survival although it is not to be taken for granted that the right season was chosen in every case, and the seeds, tubers, corms, rhizomes or shoots were inserted and cared for with a negligible amount of preparation of the soil or of subsequent tillage.

A list of the species which have been dealt with in the experiments is given below, and includes a total of 139 seed plants. If survival in the new habitat occurred this is denoted by *S* in the proper column. Species native to the regions about the four plantations are denoted by *N* in the proper column.

---

[4] Bonnier, G., "Note sur les cultures comparées des mêmes espéces à diverse altitudes." Bull. d. l.' Soc. botan. d. France, p. 467. 1887. "Étude expérimentale sur l'influence du climat alpin sur la végétation et les fonctions des plantes." Bull. d. l. Soc. botan. d. France, p. 436. 1888. "Cultures expérimentales dans les Alpes et les Pyrénées." Rev. gén. d. Botan. 11: 513. 1890. "Recherches expérimentales sur l'adaptation des plantes au climat alpin." 1895.

List of species introduced into experimental plantations

Unsuccessful introductions denoted by *.
Establishment and survival denoted by S.
Habitat from which plants were taken denoted by N.

	Coastal Laboratory	Desert Laboratory	Xero-montane plantation	Montane plantation
Abutilon Abutilon (L.) Rusby	*	N	*	
Abutilon crispum (L.) Medic		N	*	
Actæa rubra (Air.) Willd.	*			
Actæa viridiflora Greene	*			N
Aesculus Californica (Spach.) Nutt.	N		*	
Aletris farinosa L.				*
Amaranthus palmeri Wats.		N	*	
Amsinckia spectabilis F. & M.		N	*	
Apios Apios (L.) MacM.	*			*
Argentina Anserina (L.) Rydberg	N			*
Aquilegia chrysantha A. Gray	*			N
Aquilegia canadensis L.				*
Arisaema Dracontium (L.) Schott.	*			*
Arisaema triphyllum (L.) Torr.	*			*
Astragalus nuttalianus D.C.		N	*	
Audibertia stachyoides Benth	N		*	
Bicuculla cucullaria (L.) Millsp.				*
Bigelovia hartwegii A. Gray		N	*	
Bowlesia lobata R. and R.		N	*	
Brodiaea capitata var. *pauciflora* Wats.	*	N		
Cassia covesii Gray	*	N	*	
Cassia leptocarpa Benth.		N	*	
Cassia Marilandica L.	*	*		
Carnegiea gigantea (Engelmann) Britton and Rose	*	N	*	
Ceanothus thyrsiflorus Esch.	N		*	
Cercidium torreyanum (Wats.) Sargent	*	N		
Chlorogallum pomeridianum Kunth.	N		S	
Cissus sp.	*	*	S	
Covillea tridentata (D.C.) Vail	*	N	*	
Cyclanthera dissecta	*	N		
Cryptanthe barbigera (Gray) Greene		N	*	
Cleistoyucca arborescens (Torr.) Trelease	*			
Daucus pusillus Mich.		N	*	
Dentaria diphylla Mich.	*			
Dugaldia hoopesii (Gray) Rydberg	S	*	*	N
Dryopteris filix-mas (L.) Schott.	*			
Echinocactus wizlizenii Engelm.	*	N	*	
Encelia farinosa A. Gray		*		
Eriophyllum staeachadifolium Lag.			*	
Fagus grandifolia Ehrh.	*			
Festuca octoflora Walt.	*	N		
Festuca setaflora		N	*	
Fouquieria splendens Engelm.	S	N	*	
Fragaria Californica Cham. and Schlecht.	N	*		
Fragaria chiloensis (L.) Duchesne	S			
Fragaria ovalis (L.) Rydberg	S	*	N	
Fragaria vesca L.	S	*		S
Fragaria virginiana Duchesne	S			S
Franseria deltoidea Torr.		N	*	
Franseria speciosa Dougl.	*	N		
Fraxinus Americana L.	S			
Geum Canadense Jacq.	S			
Gleditsia triacanthos L.	*			
Hamamelis virginiana L.	S			*
Harpagonella palmeri A. Gray		N	*	

List of species introduced into experimental plantations—Continued

	Coastal Laboratory	Desert Laboratory	Xero-montane plantation	Montane plantation
Helianthus petiolaris Nuttall		N	*	
Hepatica Hepatica (L.) Karst.				S
Hilaria cenchroides H.B.K.		N	*	
Jatropha angustidens (Torr.) Muel. Arg.	*		N	
Juglans californica quercina Babcock				*
Juglans major (Torr.) Hell.	S			N
Juglans sp.	S	S		
Kallstroemia grandiflora A. Gray	*	N		
Isocoma hartwegii (Gray) Greene		N	*	
Lesquerella gordoni (Gray) Wats.		N	*	
Lilium superbum L.				*
Liriodendron tulipifera L.	*			
Lobelia inflata L.	*			
Lysimachia producta (A. Gray) Fernald	S			
Lysimachia terrestris (L.) B.S.P.	S			*
Machaeranthera tanacetifolia (H.B.K.) Nees	*	N	*	
Menispermum canadense L.	*			*
Menodora scabra Gray	*	N		*
Megarrhiza californica Torr.	N	*	S	
Microseris linearifolia (D.C.) A. Gray	*	N	*	
Mollugo verticilata L.			*	
Neobeckia aquatica Greene	*			*
Oenothera biennis L.	S	*	*	*
Oenothera Hookeri T. and G.	S			N
Oenothera Lamarckiana × *O. cruciata* Nutt. No. 3.21	S			
Onoclea sensibilis L.	S			
Opuntia arbuscula Engelm.	*	N		
Opuntia covillei Britton and Rose	S		S	
Opuntia discata Griffiths	S	N	S	
Opuntia discata × *laevis*		N	S	
Opuntia fulgida Engelm.	S	N		
Opuntia leptocaulis De Candolle	*	N		
Opuntia laevis Coulter	S	N	S	*
Opuntia opuntia (L.) Karsten	S	*	*	
Opuntia phaeacantha Engelm.	*	N		
Opuntia santa-rita (Griff. and Hare) Rose	S	N		
Opuntia toumeyi Rose	S	N		
Opuntia treleasei Coulter	S			
Opuntia versicolor Engelm.	*	N		
Opuntia vivipara Rose	*	N		
Opuntia sp. (edible fruit)	S	S	N	
Opuntia sp. (from 2500 M. Sta. Catalina Mts.)		S		
Osmunda cinnamomea L.	*			
Osmunda Claytoniana L.	*			*
Osmunda regalis L.	*			
Parkinsonia aculeata	*	N		
Parkinsonia microphylla Torr.	*	N		
Parthenium argentatum A. Gray	S	S		
Parthenocissus dumetorum var. *laciniata* Rehder	S		S	
Penstemon acuminatus Dougl.	*			
Penstemon barbatus (Car.) Nutt.	S	N		
Penstemon grandiflorus Nutt.	*			
Penstemon torreyi Benth.	S	N		
Penstemon wrightii Gray	*	N	*	
Phytolacca decandra L.	S	*	*	*
Pistachio atlantica	S			
Pilocereus thurberi		S		
Podophyllum peltatum L.	*			S
Plantago fastigiata Morris		N	*	

List of species introduced into experimental plantations—Concluded

	Coastal Laboratory	Desert Laboratory	Xero-montane plantation	Montane plantation
Potentilla thurberi A. Gray	S			N
Potentilla subviscosa Greene	*			N
Pteridium aquilinum (L.) Underw.	N			*
Quercus heterophylla Michx.	*	*		
Quercus hypoleuca Engelm.	S	*	N	
Quercus reticulata Hamb. and Bonpl.	S		N	
Quercus Rudkinii Britton	*			
Rhamnus ursina Greene	S		N	
Rhamnus californica Esch.	N		*	
Ribes pinetorum Greene	S			N
Rivina portulacoides Nutt.	*	N		
Robinia Neo-Mexicana S. Gray	*	*		N
Rudbeckia laciniata L.	S			N
Sanguisorba canadensis L.	*			*
Sanguinaria canadensis L.	*			*
Sarracenia Drummondii	*			
Salomona biflora (Walt.) Britton	*			*
Scrophularia leporella Bicknell	S			S
Scrophularia parviflora Woot. and Standl.	S			N
Sequoia gigantea Dec.				*
Sedum stelliforme S. Wats.	S		*	N
Selaginella rupestris (L.) Spina				*
Senecio Neo-Mexicana Greene	*			N
Solanum eleagnifolium Gar.	S			
Solanum Heegeri	*			
Solanum lanceolatum	S	S		
Solanum Fendleri A. Gray	*	*		N
Solanum rostratum Dunal.	*			
Sphaeralcea pedata Torr.		N	*	
Streptanthus Arizonicus Wats.		N	*	
Stachys sp.				*
Tradescantia scopulorum Rose	S			N
Trillium sessile angustifolium Torr.	*			
Trillium sessile L.	*			
Trillium undulatum Willd.	*			*
Verbascum Thapsus L.	S	*	*	S
Veratrum Californicum Durand	S			
Vitis Arizonica	S	N		
Vitis labrusca L.				*

Survivors are taken to include species of which individuals were alive at the time of the preparation of this paper (midsummer, 1920) after being under observation for ten to fourteen years; also a few other cases such as Fragaria at the Coastal Plantation, in which, after ample capacity for growth and reproduction had been shown, the plants were removed to make way for tests of other species.

Survivals include two classes of widely different values in dissemination. One group includes long-lived individuals, Vitis, Juglans, Sanguisorba, etc., which, having been brought in by seeds or propagules, show the expected long life of the species, and which may not propagate or have any successors.

The other group, including Fragaria, Potentilla, Scrophularia, Verbascum, Opuntia, etc., establish themselves and extend themselves by seeds, offsets and other propagules in establishment in the newly found habitats.

Most closely contrasted in behavior with the species of this group are those which like Arisaema and Trillium, show a vigorous growth, producing seeds and plantlets for periods of five years or more, but ultimately disappear. These are to be regarded as in the critical region of selection where even such a fortuitous circumstance as the character of a series of seasons may make for extinction, while if introduced two or three years later, they might have become established. Features of this kind probably characterize the fluctuating boundaries of many species.

General Considerations

A review of the records of even the successful species would extend this paper far beyond the space available for its publication. The following discussion is therefore limited to a presentation of a few of the more striking environic reactions, and to the presentation of some conclusions which bear upon dissemination, adaptation and survival of plants moving into new habitats.

Environic Reactions.—The establishment of some of the introduced species was accompanied or perhaps made possible by variations in habit and morphogenic procedure of no little interest. It is also to be said that the facts presented by unsuccessful species are scarcely less important. The principal features in the behavior of a few forms are given below.

Failure by Depletion of Storage Organs.—It has already been noted that of the ten species introduced by bulbs and corms only one survived or became established. This category included *Arisaema triphyllum, A. Dracontium, Brodiaea capitata* var. *pauciflora, Bicuculla cucullaria, Lilium superbum,* and two Trilliums.

The behavior and fate of such plants may be illustrated by the history of *Arisaema triphyllum.* About 40 corms were put in the Montane plantation in 1906, some of which matured friuts and seeds in 1907. Seedlings were seen in 1909. Representation seemed to be dwindling and 100 additional corms were added in 1913, which mostly perished in 1914. Introductions in equivalent numbers at Carmel resulted in seed-formation and some young plants, but the balance of stored food diminished year by year and no lot of plants survived more than 7 years. One plantlet had a trifoliate leaf in 1911 and 1912, but bore one with four leaflets in 1913.

Brodiaea did not last through the second season at Carmel. *Arisaema Dracontium* with its large corms introduced at Carmel in 1909 made its final showing of leaves in 1913, and survived one year longer in the Montane plantation. *Bicuculla* survived five years in the Montane plantation before its reserves were exhausted. Corms of *Trillium undulatum* did not finish the second season at Carmel, although it bloomed and matured seeds and endured 11 years in the Montane plantation before dying out.

A larger proportion of plants transferred by rhizomes and rootstocks survived, but the 23 unsuccessful species, including such plants as Apios, Menispermum, Sanguinaria, Salomona, Actaea, Dentaria and various ferns, owed at least a part of their failure to the lack of formation of rootlets with implied absorbent mechanisms. No special defect in the conditions such as illumination could be found to account for the failure to replenish the food supply. The soil moisture supply seemed adequate in such cases.

Vegetative Activity and Supernumerary Organs.—The transferrals resulted in a development of rootstocks, shoots and flowers which in some cases were notably different from that exhibited by the species in their native habitats. The behavior and formation of an extra leaflet by Arisaema has been mentioned above. *Fragaria californica* taken to the warmer and more arid climate of Tucson developed one or two extra leaflets. *F. ovalis* from the Montane region showed a similar departure both at Tucson and at the coastal plantation. *F. virginiana* did not make extra leaflets at the Montane plantation, but did so under the simulating environment at the coast, also showing some ascidial leaves. *F. californica* from the coastal region likewise formed ascidial leaves when under the influence of unaccustomed conditions, including high temperatures and aridity, at the Desert Laboratory.

The peculiar habit of the witch-hazel, *Hamamelis virginiana* in its original habitats made its behavior in these experiments an object of much interest. A dozen shrubs from New Hampshire half a meter high were put in the Montane plantation in September, 1909, and, all of these having perished by the autumn of 1912, a second lot was brought in as a spring introduction in May, 1913. Two of these were alive in 1917 but had not produced flowers and fruit and had perished before 1920.

Of the introductions at Carmel in 1909 those set out on a dry cool northern slope among the pines perished, but a dozen in the loose, moist sandy soil of the garden all survived. Britton and Brown (Illus. Flora of Northern U. S. and Canada, 2:235, 1913) note that these shrubs bloom in the period from August to December in northern and eastern United States and Canada, and in January to March in the southwestern part of the range which includes Texas.

The material used in these observations was from stock accustomed to autumnal blooming. Growth of the branches and formation of leaves in the coastal and Montane plantations came with the advent of the warmer season, which began in April at the first named place. No departure in such purely vegetative activity of the plant is to be noted.

Flowers were matured at this place as early as July 11 in some years, and not later than August 1, except in 1918 and 1919, years which were characterized by low rainfall and deficient ground water. Vegetative activity was thus followed by blooms after a period of a hundred days or more, which also may be inferred of the shrub in its native habitat.

The plant is reputed to accomplish pollination in its northern habitats in the autumn; but fertilization does not take place until spring, the fruits not reaching maturity until about the time of the next flowering stage. No information is available as to this feature in southern localities.

It was found that fruit-formation required a definite period or rather temperature exposure. Thus in years in which flowers were formed in July, fruits were matured and dropped in January and February, about six months after flowering began, the development of the fruits taking place rapidly in the warm days in September and October.

Flowers were not formed in 1918 and 1919 until August and September. Consequent upon this, green fruits of adult size were seen on some plants in June, 1920, at least nine months after flowering, and their total period on the plant would be practically equivalent to that of the plant in its native habitat.

It is a well-known physiological fact that flower and fruit formation are based upon complicated metabolic processes and that a certain supply of moisture and temperature are required to complete these processes. If the flowers are so late as to delay fruit formation until the cooler season, a longer time would be required. Early blooming brings the entire procedure within a single season in accordance with the habits of a majority of seed-plants.

The experiments with the river-cress, *Neobeckia aquatica,* were begun in 1902, and plants were subjected to a wide range of conditions in the laboratories at Carmel, at Tucson, in the New York Botanical Garden and in the Botanical Laboratories at Cinchona, Jamaica. Plants were grown in the open in the Montane and coastal plantations. Full development of flowers and fruits were secured at the coastal location only. A wide range of morphogenic reactions of this plant were summarized by the writer as follows:

"The cultivation of Neobeckia as a terrestrial was accompanied by the development of thickened roots, in which an exaggerated formation of cortical and fibrovascular tissues ensued. Large amounts of starch accumulated in these members, the entire reaction being one which probably does not occur in nature.

"Variations in the form of nepionic leaves have been seen to be coupled with the composition of the medium or subtratum, the availability of a supply of food to buds and with competition. No connection was established between the form of such organs and the stage of the material taken for rejuvenescence, although it is to be said that in most of the experiences such effects would have been masked by other effects. While it is true that most of the diverse structures exhibited by the leaves of Neobeckia show some degree of suitability to the conditions under which they are formed, yet this is by no means always the case, as instanced by the occurrence of terrestrial types in submerged plants."[5]

---

[5] MacDougal, D. T., "The Determinative Action of Environic Factors upon *Neobeckia aquatica* Greene." Flora, 106: 265. 1914.

Phytolacca decandra failed in the Montane plantation, the temperature and moisture conditions not being such as to permit the repletion of stored food-material or the development of flowers. The temperature at the Coastal plantation was also so low and so near the critical point that flowers and fruits were produced only on branches lying in a sheltered position on the ground, on plants in shelters, and in the warm dry season of 1918.[6]

The chief departures exhibited by Phytolacca were at Tucson. One consisted in galls in which two insects were found possibly acting as causal agents, the other included a wide variety of antholyses. Separate pistils, conjoined and open pistils, gynophores, flowers superimposed in senes, phyllody of the stamens and replacement of ovules by shoots, etc.[7] These abnormalities may be referable also to temperature conditions influencing the metabolism which is fundamental to the order of procedure in the morphogeny of the reproductive organs.

Rudbeckia laciniata from the region of the Montane plantation is a form designated as a separate species, *R. ampla,* by A. Nelson.[8] When grown in the coastal plantation it attained the maximum size as to leafy stems, and rootstocks. This vigorous vegetative activity did not interfere with the maturation of an abundant crop of seeds. One plant formed flowers of a greenish hue in 1918.

Scrophularia leporella from Staten Island, N. Y., and material of a closely related species (probably *S. parviflora* Woot. and Standl.) were established in the coastal plantation in 1912, where a luxuriant development of shoots and thickened roots was accompanied by the formation of an abundant crop of viable seeds. This vigorous growth was accompanied by the development of some peloric flowers, and by the formation of extra divisions of the corolla and an extra stamen. Thus one flower was preserved that had 10 divisions of the corolla, 2 extra inner petaloid organs, 9 divisions of the calyx and 8 stamens. The sterile stamens in such divergent flowers were seen to contain perfect pollen in many cases. Still another series of aberrations in leaf-form and flower-color in plants arising from seeds developed in ovaries treated with chemical solutions have been previously described.[9]

The wild potato of Arizona, *Solanum Fendleri,* was successfully grown from both seeds and tubers at the Coastal plantation. Flowers were successfully pollinated from the cultivated potato of the region in 1914, which resulted in a unified hybrid which has reproduced by both seeds and tubers in the succeeding seasons. The hybrid shows irregularities of flowers and of leaves.

---

[6] See Lloyd, F. E., "Critical Flowering and Fruiting Temperatures for *Phytolacca decandra.*" Plant World, 20: 121. 1917.

[7] Lloyd, F. E., "Response of *Phytolacca decandra* to Various Environmental Conditions." Rep. Dept. of Bot. Res. Carnegie Inst. of Wash., p. 71. 1914.

[8] Bull. Torr. Bot. Club, 28: 234. 1901.

[9] MacDougal, D. T., "The Experimental Modification of Germ-plasm." Ann. Mo. Bot. Garden, 2: 253. 1915.

A woody Solanum (*S. lanceolatum*) from Tehuacan in the arid highlands in southern Mexico exhibits an extremely vigorous development of underground members, of leafy shoots, and of abundant fruits containing viable seeds both at the Desert Laboratory and at the Coastal Laboratory. Propagation is carried on by underground stems the tips of which give rise to shoots at distances of several meters from the parent plant. The leaves presented a simpler outline than those of plants in the original habitat of the species.

The well-known weed *Verbascum thapsus* also showed great vegetative activity as well as abundant seed formation at the Coastal plantation. One of the results of such action was the development of tall shoots which perennated, blooming continuously for three or as long as four years. This long-continued growth was carried out by the development of buds in the axils of the upper narrower leaves on the flowering shoots. It is to be noted that this plant has come to occupy great areas in regions to the northward and eastward of the Coastal plantation.

Some comprehension of variations which may take place in a plant as a change of habitat may be gained by a consideration of the differences in the carbohydrates of an Opuntia grown at the Desert Laboratory and at the Coastal Laboratory which are shown in the following table:[10]

Carbohydrates of Opuntia	Coastal percent.	Desert percent.
Water	91.15	80.34
Total sugars	2.61	4.30
Total polysaccharides	1.94	3.50
Hexose polysaccharides	.09	1.65
Disaccharides	.07	.04
Hexoses	.52	.06
Pentoses	.14	.05
Pentosans	1.70	1.74

As the development of almost all organs depends upon the existence, not of certain substances alone, but of groups of substances in certain proportions, the wide variations in the dissacharides, hexoses, and pentoses would inevitably be followed by altered procedure on the part of the plant. Similar differences are amply illustrated in agricultural literature.

COMPARATIVE VALUES OF VARIOUS TYPES OF DISSEMINULES IN SURVIVALS IN NEW HABITATS: *Receptivity of New Habitats.*—The following generalizations are supported by the detailed records of the species in the several habitats.

1. Seeds and living plants of 139 species were used in the introductions into the four locations, and the behavior of these plants has been followed during the 14-year period from 1906 to 1920.

---

[10] Taken from MacDougal, D. T., "Hydration and Growth," p. 133. Publ. 297, Car. Inst. of Wash. 1920.

2. Several of the above species were put in more than one plantation, bringing the total number of tests or introductions to 192. The repetition of introductions brings the total number of operations to about 250.

3. The Montane plantation showed establishment and survival of 7 species out of 28 introductions; the Xeromontane plantation 7 out of 33 introductions; the Desert Laboratory 6 out of 21; and the Coastal Laboratory 41 out of 100 introductions. From a total of 192 introductions 60 survivals resulted, which included 50 species.

4. Only one survival resulted from introductions by bulbs or corms, out of 10, although many of these were duplicated, suggesting that this form of the resting shoot is not well adapted to dissemination or establishment in new habitats without cultivation.

5. Eight of the 31 introductions of plants which assume a resting form in rhizomes and rootstocks survived.

6. Twenty-one of the 55 species transferred as plants with resting aerial shoots survived in new locations, some in more than one.

7. Twelve of the 40 species which were carried as seeds survived in the new locations.

8. The failures represent in part perhaps faulty judgment of the operator, and in part the lack of adaptability of the species. The operator had at his command some practical knowledge of the plants in a wild condition and of the environmental conditions of the plantations. With allowances for this, it is to be seen that the greatest percentage of survivals was by plants with resting shoots, of which 38 percent survived. The successes in this form were more numerous than with seeds, which amounted to 30 percent. Twenty-six percent of plants with rhizomes and thickened roots were successful, while but 10 percent of the species which rest as corms or bulbs survived.

9. The 7 survivals in the Montane plantation comprise 3 with rhizomes and 4 with tufts of small roots with the shoot dying to ground each year. The 7 survivals at the Xeromontane plantation include three Opuntias with succulent shoots, Chlorogallum with a coated bulb, Megarrhiza with a heavy thickened underground stem and two vines, one with a rhizome and the other with a thickened underground stem. The 6 survivals at the Desert Laboratory included a Juglans brought down a vertical mile from the nearby mountains, two Opuntias similarly introduced, Pilocereus brought a hundred miles beyond its range, Parthenium from the Chihuahuan desert, and a Solanum from the deserts of southern Mexico. The most notable feature attendant upon the introductions was the large number of species from the montane region which flourish near the seashore. Fifteen species, including trees, shrubs and herbaceous perennials, survived out of a total of 18 species used in this test, making the highest proportion of successes of that of any of the operations. Of 56 species brought from the arid regions but

14 survived at the Coastal Laboratory, of which 9 were cacti. Of the other five, Fouquieria would not grow from seed and the small plants grew sluggishly. These were: the Juglans from the lower parts of the mountain water courses, Vitis from habitats along streamways with a marked underflow even in the dry season, Parthenium, a true desert shrub, and the Renstimous, likewise an inhabitant of very arid localities. Of 28 species from the Atlantic seaboard region nearly one half survived in the coastal plantation. Finally it is to be noted that not a single species from the Atlantic seaboard or the Pacific coastal region became established at the Desert Laboratory. Two species from the chaparral of the coast however became established at the Xeromontane plantation, which is in a loose chaparral association. *Opuntia Opuntia* from the eastern seaboard withstood the physical conditions at the Xeromontane plantation but was exterminated by animals. No plants from the coastal region, from the Desert Laboratory or from the Xeromontane plantation survived in the higher mountain location of the Montane plantation.

Conditions of Dissemination, and Distributional Barriers.—1. In a consideration of barriers[11] which might operate to prevent the dissemination of species from their present habitats to others in which they might thrive it is evident that all ranges of mountains "insular" to deserts are so widely separated (1,300 km. in the present instance) from coastal habitats that the chances of transportation are so small as to be of no importance.

The arrangement of disseminational agencies in the present instance is not such as allow the remotest probability of the transportation of species from the mountain to the sea by the path followed. Other and more favorable combinations might readily occur.

Whether or not montane species might persist during the long process of base-levelling and thus finally descend to the sea takes one into speculative possibilities which are by no means simple.

The occupation of seashore areas and of contiguous mountain slopes to an elevation of 1,000 meters or more on the Pacific Slope is exemplified by such species as *Quercus densiflora, Q. Kellogii, Q. chrysolepis, Torreya californica, Umbellularia californica, Arbutus Menziesii, Pseudotsuga taxifolia, Acer macrophyllum, Prunus demissa, P. subcordata, Rubus grandiflorus,* and *Heuchera micrantha.*[12] As the warmer and southerly part of the range is reached, however, these species do not occupy the coastal areas. Nor have any instances been cited where a species showed a pattern of distribution similar or parallel to that brought about in the experiments by which species occupied mountain tops and coastal regions of the same land in about the same latitude.

---

[11] MacDougal, Richards and Spoehr, "The Basis of Succulence in Plants." Bot. Gaz. 67: 405, 1919, and MacDougal, "Origination of Xerophytism." Plant World, 21: 245. 1918.

[12] List furnished by Miss Alice Eastwood of the California Academy of Sciences.

2. The inversions of temperature, which are so noticeable in arid mountainous regions, are markedly illustrated by the records at the Desert Laboratory,.and the Montane plantation 20 miles distant. The minimum on the shoulder of Tumamoc hill at 820 meters in the winter and spring season at which time such differences are critical is often 6° or 7° C. above that of the garden at the foot of this hill a hundred meters lower, owing to the drainage of cold air from the tributary slopes and cañons.

So pronounced is this action that the minimum here, — 12° C., is lower than that of the Xeromontane plantation nearly a thousand meters higher on the mountain slopes across the valley. Still more remarkable, however, is the fact that this minimum is lower than that of the Montane plantation at 2,600 meters (— 7.5° C.) where the snow lies several months each year and the number of days of cold are many times that of the region about the Desert Laboratory.[13] The possibility of such inversion as a factor affecting distribution was first proposed by the author in 1898, and a study of such effects has been made by Dr. Forrest Shreve.[14]

3. The dissemination of species toward lower levels takes place with facility, as the change is from low to higher temperatures, and the actual transportation of seeds or propagules would be aided by air currents, gravity and resulting earth and rock slides and streams of water. The isolated mountain and desert complexes, however, offer a range of temperatures beyond the capacity for adaptation of all but a few foreign species. Some of the oaks descend far along the streamways, supporting the suggestion that of the millions of acorns which are carried down some must in all probability have reached every place in the drainage where the adult might survive. All of the walnut (*Juglans major* Torr. Hell.) extending from 800 meters at the foot of the Santa Catalina mountains to 2,500 meters is included in one species by many systematists. The nuts from trees at the lower and the higher levels taken to the Coastal plantation develop into trees easily separable as to form and behavior. They are not so widely separated, however, but that they may be considered as segregations of characters within a species in the broadest sense.

It seems reasonable to assume that the major habitat of this tree lies in climatic complexes more like those of the higher levels, and to infer that the strain or species in the lowlands is a survival by some departure from the parental stock.

4. An action the reverse of this may be found in the distribution of some of the Opuntias. These are preeminently characteristic of the lowlands, and of the deserts. A half dozen species, however, are represented in the

---

[13] The same interesting phenomenon is found in the San Francisco Mountains of Arizona. See Pearson, "Factors Controlling the Distribution of Forest Types, Part I," ECOLOGY, Vol. 1, No. 3, pp. 139–159, 1920, especially p. 150.—ED.

[14] Shreve, F., "Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors." Publ. Carnegie Inst. of Wash. No. 217. 1915. See p. 82.

region of the oaks as high as 1,700 meters, while one species extends beyond the oaks and is found among the pines on rocks at 2,300 meters. Joints of this plant brought down to the base of the mountain thrive although placed a mile below the level of their highest occurrence. In fact all of the species of Opuntia of the mountain slopes grow so well at the bases of the mountains that it is evident that their original or main habitat is at the lower level.

5. Some interesting facts bearing on the distributional advance of the Opuntias up the dry mountain slopes are available. Chief among these are the parts played by animals in modifying dissemination. The species which spreads through the oaks and up into the region of the pines is one the fruit of which is attractive to the birds, and coupled with this is the fact that at the higher levels it is found chiefly in the crevices of huge boulders and masses of rock in places but little frequented or visited by rodents or other animals using plants as food. The entire distribution of the plant might be accounted for on the supposition that it is carried from point to point by birds, and as it matures seeds even at the higher levels it seems destined to maintain itself throughout its present range. Animals in this case bear a part as a disseminating agency. It was discovered, however, that other animals, probably rodents or rabbits, operate a barrage against the movement of other Opuntias upward on the mountain slopes as became evident by some experimental tests in the Mohave desert of California and by repeated introductions at the Xeromontane plantation.

The facts of interest in this connection are as follows: Three separate introductions of a half dozen species of Opuntia were made by placing several rooted plants in three places in successive years near the vicinity of Barstow, California, primarily for the purpose of making observations upon the behavior of plants native to a desert with summer as well as winter rainfall when transferred to a region in which the major precipitation is in the cooler season. In all cases the plants were quickly devoured by the native rodents, and it was seen that these animals would constitute an effectual barrier against the movement of these Arizona plants into the Mohave desert. The next evidence in this connection consisted of the results obtained from *Opuntia Opuntia,* the small spineless species from the Atlantic seaboard. Plants survived in the Coastal plantation and when put in the plots at the Desert Laboratory, at the Xeromontane plantation and at the Montane plantation, quickly disappeared from the Xeromontane location, although surviving both above and below this place. The first introduction into these three places was made in 1906 and since that time three large lots have been placed in the Xeromontane plantation with similar results. A platyopuntia (*O. covillei*) and a cylindropuntia native to the mountains of southern California had a similar fate, those inside the screen surviving while those outside were eaten (see fig. 2).

Opuntia laevis is found in the foothills below the Xeromontane plantation but has not been seen by the author among the oaks. It was first taken to the Xeromontane plantation in 1915, a second lot in 1916 and a third lot in 1917. All were eaten before the close of the season.

Finally wire screened cages were put in the Xeromontane plantation for the purpose of testing the behavior of these and other plants when protected from the large animals. The fourth introductions made in the spring of 1918 show that *O. laevis* thrives in this location when thus protected, while of the lot outside the screen but one small remnant was seen in the fall of 1919. Two hybrids of *O. discata* × *O. laevis,* Nos. 3 and 7, were taken to the Xeromontane plantation in 1915 and were destroyed by animals in 1915, and a second lot met the same fate in 1916. After a third lot was placed in and outside the screens in 1917 the experiences with *O. laevis* were duplicated.

The foregoing set of observations furnish evidence of a fair degree of conclusiveness that the small animals native to the zone of the oaks in the Xeromontane region effectually limit the distribution of *Opuntia laevis,* and the destruction wrought on other species might have a similar final effect.

6. It is rarely possible to ascribe the stoppage or restriction of a species to the direct and simple action of a single physical agency. The actual effect of defective humidity, low or high temperatures, soil moisture, and other environic components, each is modified in a manner by the intensity or degree of the others, together with an allowance for rapidity of variation in these factors as well as time or duration of exposure.

7. It can not be said that the vegetation of the principal land areas shows that the movements of species are chiefly from colder to warmer regions, yet it is obvious that in any series of experiments species from cool regions may be more easily established in warm places than the reverse, and montane plants may come to the seashore more easily than the plants of maritime zones may spread over a mountain.

Disseminational movements are seen to be freer when they are from regions presenting climatic extremes to more equable climates, as amply illustrated by the success of so many species from the Atlantic states and Arizona highlands on the Pacific seashore. Possibly the occurrence of the succulent Opuntia in Saskatchewan may be considered as an example of this as the predominant feature in dissemination.

8. In any discussion of movements from one region to another it is to be noted that not all groups of forms move with the same facility. Thus the species characteristic of desert regions represent an extreme development toward succulence and xerophytism suitable for existence with a lessened water supply, and the retracement of the long way of morphogenic alteration by such species is all but impossible. On the other hand many mesophytic plants show direct or individual alterations by which they pass into arid areas and maintain themselves for extended periods.

9. The experiments again make it plain that the habitat in which a plant may be found, or in which it may have originated, may not furnish the most favorable environmental complex, as amply illustrated by the behavior of species that have become weeds. In other words the fitness of a species for its native habitat may not be so close as its fitness for other, as yet untried conditions.

SUMMARY

Experimental areas with widely differing environmental complexes were established: (1) at 2,500 meters elevation in a coniferous forest on the Santa Catalina mountains of southern Arizona; (2) at 1,700 on the same mountains in the zone of sclerophyllous trees and shrubs; (3) at the Desert Laboratory near the base of these mountains; and (4) at the Coastal Laboratory in the summer-fog section of the California coast.

Seeds and living plants of 139 species were introduced into these four areas; the number of introductions is 192, and with repetitions the operations total 250. Most transfers were from one area to another, but some plants came from eastern United States, and one from Mexico. The behavior of these plants has been observed for 14 years, from 1906 to 1920.

The Montane plantation showed the establishment and survival of 7 species out of 28; the Xeromontane of 7 out of 33; the Desert Laboratory of 6 out of 21; and the Coastal Laboratory of 41 out of 100.

The greatest percentage of survival, 38 percent, was shown by plants transferred as resting aerial shoots; of the transfers by seed 30 percent survived; rhizomes and thickened roots gave 26 percent; while corms and bulbs showed only 10 percent.

Transfers from the montane zone to the coast had the largest proportion of survival, 15 out of 18 species. Of 56 transfers from the arid stations to the coast only 14, 9 of which were cacti, survived. No species from the Atlantic seaboard or Pacific Coastal region survived at the Desert Laboratory. No plant from the Coastal region, from the Desert Laboratory or from the Xeromontane station survived at the Montane plantation. Nearly half of the 28 species from the Atlantic seaboard introduced at the Coastal station survived.

The plants transferred developed in some cases rootstocks, shoots, and flowers notably different from those of their native habitats. The unsuccessful species showed behavior scarcely less important than the successful.

Animals act as a barrier to the upward extension of certain Opuntias by devouring the plants.

Disseminational movements are freer when they are from regions of climatic extremes to more equable climates.

The habitat in which a plant may be found is not necessarily the most favorable environment for it.